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Modelling the effects of different quality prey fish species and of food supply reduction on growth performance of Roseate Tern chicks

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Abstract

We assessed the effects of different quality fish species and reductions in their abundance in the growth of Roseate Tern (*Sterna dougallii*) chicks in the Azores. An energetic balance model was developed, which accounts for the energy available from ingested fishes and the energy expenditure by the chicks. Fish species ingested by Roseate Tern chicks were mainly *Trachurus picturatus*, *Scomberesox saurus*, *Macroramphosus scolopax* and *Capros aper*. Energy expenditure was defined by the basal metabolic rate (BMR), which depends on chick's weight, plus a multiple of BMR, obtained by calibration and accounting for unspecified energetic losses. Real data obtained in June–July of 1996 and 1995 were used to calibrate and validate the model, respectively. Regressions between observed and predicted data showed a higher fitting level for 1996 than for 1995, which seems to be related with the need for more accurate estimations of assimilation efficiency and energy expenditure parameters. Of the four main prey species, *T. picturatus* was the most energetically favourable because of its high length–weight regression and to the capacity of chicks to swallow *T. picturatus* with an average length of 8.71 cm. *C. aper* had a higher length–weight relationship, but chicks were only able to ingest items <5 cm because this species is wider than *T. picturatus*. *S. saurus* and *M. scolopax* were energetically less efficient because they had a lower length–weight relationship. Observations suggest that the availability of less energetic fish (e.g. *M. scolopax*) leads to higher delivery rates by the parents and, consequently, to higher ingestion rates by the chicks. However, both observations and predictions suggest that the growth efficiency is lower than when the chicks were fed with *T. picturatus* with an average length of 8.71 cm. Additionally, the model predicts that chicks with 23 days of age will attain 85 and 56 g, according to a 25% reduction in prey within a year of energetically more and less favourable prey, respectively. Chicks in the first situation are still likely to fledge, while in the second case, chick survival is certainly compromised. In summary, the growth of Roseate Tern chicks in the Azores will be significantly reduced in response to a decrease in energy intake resulting from provisioning of low quality fish species and chick survival is compromised whenever this factor is associated with a significant (25%) reduction in fish stocks. This model proved to be a highly dynamic tool in assessing variations in postnatal growth of Roseate Terns in response to variations in food quality and quantity and it should be of interest in the conservation strategy of this species.

Keywords: Energetic balance model; Chick growth; *Sterna dougallii*; *Trachurus picturatus*; Fish stock reductions; Azores

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1. Introduction

Piscivorous seabirds feed on a patchily distributed resource, varying widely in abundance, in space and in time (Shealer, 2002). The quality of fish prey for seabirds also can vary significantly due to a complex set of characteristics such as mass, length, width, energy content (mostly related with the amount of lipids) and presence of large spines (Shealer, 2002; Dahdul and Horn, 2003). A supply of fish of adequate quality is particularly important during reproduction, in order for parents to ensure that their offspring reach independence in good condition. Variation in food supply, both in terms of quantity and quality, have a strong impact on productivity of marine birds with small foraging ranges such as marine terns *Sterna* sp. (Safina et al., 1988, 1990; Monaghan et al., 1989; Massias and Becker, 1990). In physiological terms chick growth is compromised by a decrease in food intake (Schew and Ricklefs, 1998). The effects of strong reductions in food supply on productivity and growth of marine terns has been well documented, with strong crashes in prey fish stocks leading to breeding failure of entire seabird colonies (Monaghan et al., 1992).

Chicks provisioned on a reduced amount of food exhibit slower growth and have a longer nestling period (Visser, 2002). Variation in chick growth in relation to the ingestion of prey differing in quality has received less attention. This is particularly important if, for example, the most abundant prey is low in energy, too small or deep-bodied (i.e. difficult to swallow by young chicks). In the Azores archipelago, North Atlantic Ocean, four to five species of small fishes, trumpet fish (*Macroramphosus scolopax*), blue jack mackerel (*Trachurus picturatus*), boarfish (*Capros aper*), garfish (*Belone belone*) and lanternfishes (especially *Electrona rissoi*) are important prey for a variety of predators, including fish, sharks and seabirds (Granadeiro et al., 1998, 2002; Ramos et al., 1998a,b). These prey fishes show significant spatial annual variation in their importance in the diet of seabirds, including marine terns such as the Roseate Tern (*Sterna dougallii*) (Ramos et al., 1998a,b; Granadeiro et al., 1998, 2002; Meirinho, 2000). This may be connected to temporal and spatial variation in the abundance of prey fishes. Azorean Roseate Terns seem obliged to switch between prey types among years and along a specific season as their chicks grow. *M. scolopax* and *C. aper* are deep bodied and, thus, too wide for young chicks to swallow (Ramos et al., 1998b), whereas *T. picturatus* and *B. belone* are elongated fishes. In addition, *M. scolopax* and *C. aper* have acute dorsal fins, which may kill small chicks and have a lower calorific content (Ramos et al., 1998a,b; Pereira, 2002). Altogether, these aspects make Roseate Terns in the Azores a good subject to evaluate the effects of changes in prey composition on chick growth.

Using an energetic balance model, we examined the effects of ingestion of prey fish species differing in quality on the growth performance and weight at fledging of Roseate Tern chicks. The model was also used to assess the impacts of food supply reductions on the growth of Roseate Tern chicks. The use of energetic balance models in seabirds feeding ecology may be an alternative and/or complementary approach to difficult protocols where chicks are raised in the laboratory on a limited number of fish species previously captured (e.g. Dahdul and Horn, 2003). On the other hand, because it emphasises the energetic dependency of birds on its prey species, such type of analysis may be of important value for the conservation of seabirds, namely Roseate Tern, which is a species of conservation concern in Europe (Hagemeijer and Blair, 1997).

2. Methods

2.1. Data sets

The model was built with data from a study on the feeding ecology of Roseate Tern (*S. dougallii* Montagu) chicks on Vila Islet, Santa Maria, Azores (36.9°N 25°W), in June–July 1996 (Pereira, 2002). Nests with pipping eggs or newly-hatched chicks of known age were fenced with 0.5 m high, 1.5 m in diameter (and lined with 10 cm high of 1.5 cm^2 mesh plastic wire and dried grass) and observed from a portable hide situated 4–10 m away from the nests. Chick ingestion rate (number of fish h^{-1}) was obtained from 07:00 to 9.30, 11.45 to 14:15 and 17:00 to 19:30. These three periods captured the daily variability in chick food provisioning (Ramos et al., 1998b). Field ingestion rates were corrected for a total of 13 h, corresponding to the number of hours of daylight that parents deliver food to chicks at this time of the year. Ingested fish were identified

Table 1
Total length (TL, cm)–weight (W, g wet weight) regressions for the fish species used in the model

Species	Regression	*N*	Local	Reference	Standard caloric
Trachurus picturatus	$W = 0.00819 \times TL^{3.11}$	2530	Faial and Pico Islands-Azores	Isidro (1990)	3.809
Scomberesox saurus saurus	$W = 0.0079 \times TL^{2.54}$	18	Santa Maria Island-Azores	Pereira (2002)	3.851
Macroramphosus scolopax	$W = 0.0040 \times TL^{3.15}$	34	Balearic Islands	Merella et al. (1997)	3.934
Capros aper	$W = 0.0282 \times TL^{2.81}$	104	Balearic Islands	Merella et al. (1997)	3.181
Myctophum punctatum	$W = 0.0905 \times TL^{3}$			Pauly (1980)	3.641
Pagellus bogaraveo	$W = 0.0104 \times TL^{2.891}$	57	South west coast of Portugal	Gonçalves et al. (1997)	3.348
Cubiceps gracilis	The same as *T. picturatus*				3.809
Non-identified	The same as *T. picturatus*				3.809

N, number of replicates; local, site where the replicates were collected; standard caloric, average caloric content obtained in the lab by calorimetric analysis (kJ g^{-1} ww).

to species, whenever fishes where delivered to chicks by the parents and the total length of fishes was estimated in relation to the adult Roseate Tern bill length (for further details see Ramos et al., 1998b; Pereira, 2002). Chicks were weighed every day, at 19:30 h, from the day of hatching until they were 25 days. However, because from day 24 onwards, most chicks fledged and left the fences, the model only considers the period from hatching to 23 days. The number of chicks varied from a maximum of 12 chicks with age 0 to a minimum of 3 chicks with 24 days.

During 1996 the four more abundant fish species consumed by Roseate Tern chicks were: *T. picturatus* Bowdich, *S. saurus* Walbaum, *M. scolopax* Linnaeus and *C. aper* Linnaeus. Other species, such as *Myctophum puntactum* Rafinesque, *Pagellus bogaraveo* Brünnich, *Cubiceps gracilis* Lowe and a group of unidentified fishes were also ingested but in lower amounts. From significant regressions (Table 1) obtained in the literature and in http://www.fishbase.org, it was possible to determine fish weights from measured lengths. The average caloric content of ingested fish species (kcal g^{-1} wet weight converted to kJ g wet $weight^{-1}$) was determined with a calorimeter Parr, except for *C. gracilis*, which was assumed to have the same average energetic content of *T. picturatus* because it has a similar shape. The average caloric content of the unidentified fish group was also assumed to be the same as *T. picturatus* because this was the most abundant prey fish species in 1996 (Table 1).

The model was validated with data from a study conducted in 1995 (see Ramos et al., 1998b). The experimental procedure was very similar to the one used in 1996, although the chicks were kept in a relatively smaller area (0.5 m high, 1 m in diameter, 1.5 cm^2 mesh plastic wire enclosures) and the chick's feeding behaviour was observed continuously from 07:00 to 19:00. Ingestion rates quantified in 1995 were also corrected for a total of 13 h and we assumed the same average calorific content for fish species as in 1996. In 1995, the feeding behaviour of Roseate Tern chicks was only assessed until they were 19 days and Roseate Tern chicks were not observed to ingest *P. bogaraveo* and *C. gracilis*.

Prey species ingested by chicks varied greatly between 1995 and 1996, a result attributed mainly to a switch from *M. scolopax* to *T. picturatus* (Fig. 1), which was reflected in a significant decrease in chick feeding frequency (ANOVA, $N = 172$, $F_{1,170} = 6.90$, $P < 0.05$) (Fig. 1). This difference was also reflected in the growth variation of chicks in 1995 and 1996 (Fig. 2).

2.2. Simulations and assessing model credibility

To assess which of the four main fish prey species are energetically more favourable to Roseate Tern chicks, a set of simulations was carried out where chicks were fed, separately, in only one of the four main fish species, assuming a constant ingestion rate of 4.5 fish per chick d^{-1}. To facilitate results comparison, fish length was kept constant throughout time, assuming a value, which corresponds to the average real value of each fish species. The used fish lengths were 8.71, 8.93, 4.31 and 6.83 cm for *T. picturatus*, *S. saurus*, *C. aper* and *M. scolopax*, respectively.

To assess for the simultaneous impacts of the quality of fish preys and of the reductions of prey stocks on

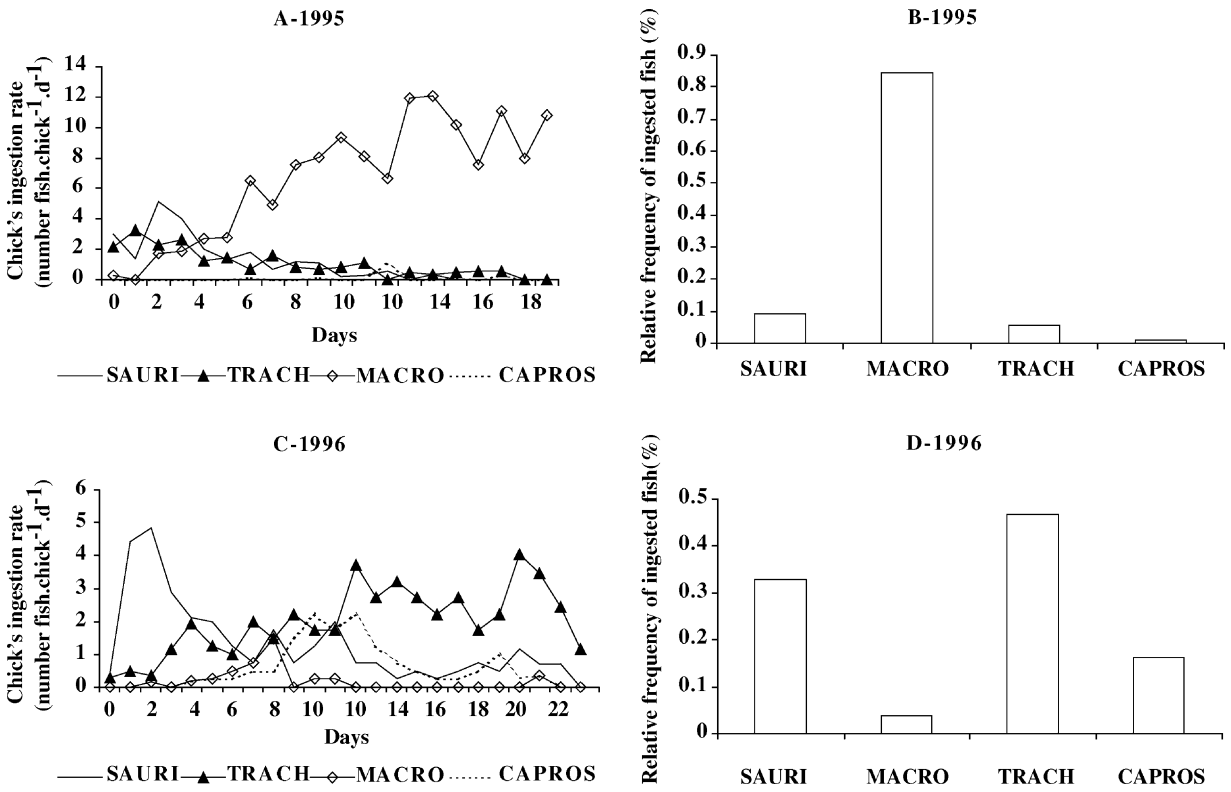

Fig. 1. Observed fish ingestion rates by Roseate Tern chicks (number of fish per chick per day) and relative frequency of ingested fish species in 1995 (A and B) and in 1996 (C and D). In 1995, the maximum ingestion rate was 12 fishes per chick per day and the most consumed species was *Macroramphosus scolopax*, while in 1996, the maximum ingestion rate was 5 fishes per chick per day and the most consumed species was *Trachurus picturatus*. Fish ingestion rates in 1995 and 1996 were significantly different (ANOVA, $F_{1,170} = 6.90$, $P < 0.05$).

the growth and weight at fledging of Roseate Tern chicks, individual simulations considering a reduction of 25% on *T. picturatus* (energetically rich prey) and of 25% on *M. scolopax* (energetically poor prey) fish ingestion rates were performed. In the first case, the model was run with data from 1996 and on the second case with data from 1995, to simulate an year with high abundance of rich-quality preys (*T. picturatus*) and high abundance of low-quality preys (*M. scolopax*), respectively.

Model credibility was assessed by regressions between the observed and the predicted data sets. Model II-regression is recommended whenever both variables are subject to error and special computation techniques are needed for its calculation (see Sokal and Rohlf, 1995, p. 543). In the present work, Model II-regressions were obtained by the method of *principal axes* because the two variables (observed and predicted) are in the same units (Sokal and Rohlf, 1995). The significance of the regressions was tested by ANOVA because analysis of variance is the only means of testing it in Model II-regression (Fowler et al., 1998). To test for the hypothesis that the inter-

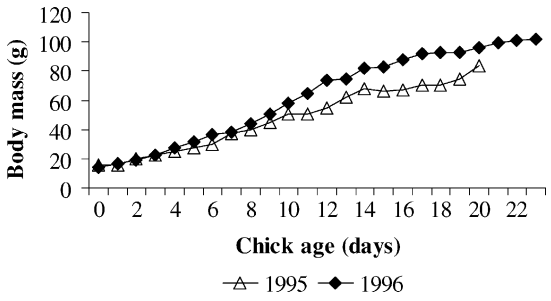

Fig. 2. Observed growth of Roseate Tern from hatching to fledging in 1995 and 1996.

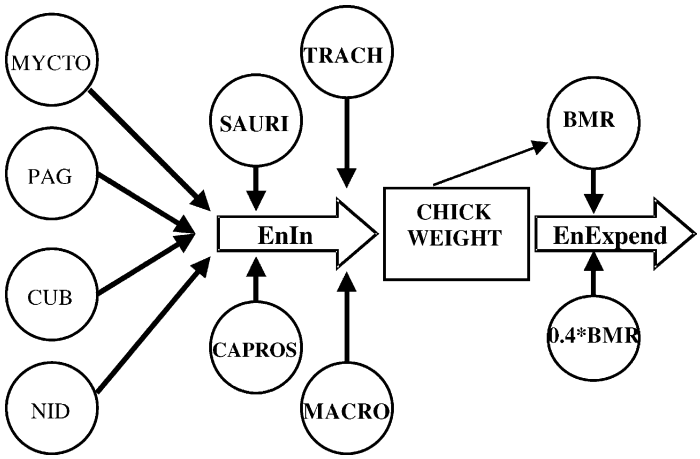

Fig. 3. Simplified conceptual diagram of the model. The model simulates the average weight of a Roseate Tern chick (CHICK WEIGHT) through out time dependent on the energy obtained from ingested fishes (EnIn) and on the energy expenditure (EnExpend). The most abundantly ingested fishes (bold) are: *Scomberesox saurus*, SAURI; *Trachurus picturatus*, TRACH; *Macroramphosus scolopax*, MACRO; and *Capros aper*, CAPROS. The less abundantly ingested fishes are: *Myctophum punctatum*, MYCTO; *Pagellus bogaraveo*, PAG; *Cubiceps gracilis*, CUB; and a group of non-identified fishes, NID. Energy expenditure (EnExpend) is defined by the basal metabolic rate (BMR), which depends on chick's weight, plus a term defined as a multiple of BMR (0.4 × BMR), which accounts for extra energetic wastes.

cept of the estimated regressions is not significantly different from 0 and the slope is not significantly different from 1, the Dent and Bleckie regression test (DBK) was used, which simultaneously tests the slope and the intercept (Dent and Bleckie, 1979).

2.3. Model conceptualisation

The model is formed by the fish modules, which estimate the energy obtained from ingested fishes and by the sub-model of Roseate Tern chicks (Fig. 3). A total of eight fish modules are considered according to data on fish prey species available for Roseate Tern chicks in the Azores in 1996. For a matter of simplification, the name of each fish module was abbreviated and derived from its Latin name: TRACH for *T. picturatus*, SAURI for *S. saurus*, MACRO for *M. scolopax*, CAPROS for *C. aper*, MYCTO for *M. punctatum*, PAG for *P. bogaraveo*, CUB for *C. gracilis* and NID for non-identified fishes. From real data, it was possible to obtain the ingestion rate of each fish species, per chick, per day. The total caloric content of each ingested fish was obtained from the fish weight and its average caloric content per gram. Fish weight was obtained from length–weight regressions (Table 1, Fig. 4). Each fish module is used to estimate the amount of energy ingested per chick, per day (kJ per chick d^{-1}). The total amount of energy ingested per chick, d^{-1} (kJ per chick per day) is the sum of the values estimated within each one of the eight fish modules. In the simulations that use data from 1995, only six fish modules were considered because, in that year, Roseate Tern chicks were not observed to ingest *P. bogaraveo* and *C. gracilis*.

The sub-model of Roseate Tern chicks estimates the average weight of a chick from hatching until fledging. Every day, the average weight of one chick is obtained from the balance between the energy input, resulting from fish ingestion, and the energy expen-

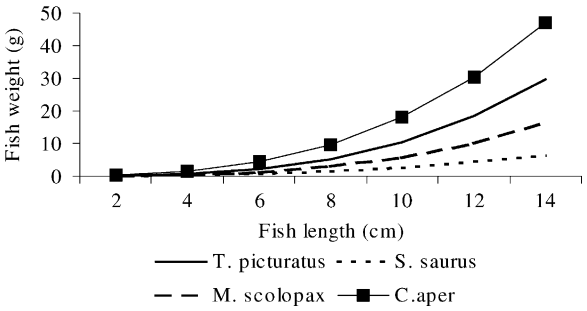

Fig. 4. Length–weight regressions for the four main fish prey species.

diture as a result of basal metabolism and other energy wastes. Flow units between the fish modules and the Roseate Tern chick's sub-model are kJ d^{-1}. In order to obtain the average daily weight of a Roseate Tern chick, a conversion factor of 7.995 kJ g^{-1} wet weight of bird (Jørgensen et al., 1991) is used in the model.

The model behaviour depends on the fish ingestion rates by the chicks (number of fish per chick d^{-1}), which depend strictly on prey delivery by adults, and on fish lengths (cm). The model state variable is the average weight of a Roseate Tern chick (g wet weight). The model was written with STELLA 7.03 software (High Performance Systems Inc., USA). The basic run uses field data from 1996, for 23 days with a DT of 1 day. The validation run uses field data from 1995, for 19 days (in 1995, the chicks were only observed until 19 days), with a DT of 1 day. All the other simulations were run for 23 days with a DT of 1 day.

2.4. Modules for fish prey species

The matrix with real data was ordered according to Roseate Tern chick's age from day 0 (hatching) until chicks fledging. For each day and for each fish species, both the number and the length of ingested fishes are known, as well as, the number of chicks of a certain age, which allowed to calculate the average ingestion rate per chick per day. As previously explained, this value was then corrected for a total of 13 h per day (IRFish, number of fish per chick d^{-1}), which corresponds to the feeding period of chicks at this time of the year. Using significant regressions, it was possible to obtain the weight of each ingested fish (FishWeight, g ww) from the measured fish length (FishLength, cm) (see Table 1) and the energetic content of each individual fish (FishCaloric, kJ g^{-1} ww of fish) was calculated by:

$$\text{FishCaloric} = \text{FishWeight} \times \text{StandardCaloric} \quad (1)$$

where StandardCaloric is the average caloric content (kJ g^{-1} ww) estimated by calorimetry (see Table 1). Because, chicks usually ate more than one fish item of each species per day, an average daily value of FishCaloric was estimated (AvFishCaloric). The total energy obtained per chick, per day, from each fish species (FishEnergy, kJ per chick per day) was calculated by

$$\text{FishEnergy} = \text{IRFish} \times \text{AvFishCaloric} \quad (2)$$

Finally, the total daily energy available from all ingested fishes (TotalFishEnergy) is calculated from the sum of all fish modules

$$\begin{aligned}\text{TotalFishEnergy} = {} & \text{TRACHEnergy} + \text{SAURIEnergy} \\ & + \text{MACROEnergy} \\ & + \text{CAPROSEnergy} \\ & + \text{MYCTOEnergy} + \text{PAGEnergy} \\ & + \text{CUBEnergy} + \text{NIDEnergy}\end{aligned} \quad (3)$$

2.5. Sub-model for Roseate Tern chicks

2.5.1. Energy available from ingested fishes (EnIn)

Some portion of the total energy ingested (I) by Roseate Tern chicks constitutes excretory energy (E), which is lost as faeces and/or urine, while the remaining portion represents metabolizable energy (ME) (Weathers, 1996). Estimated assimilation efficiency coefficients (Q) for several species of terns ranged between 0.80 and 0.83 (Klaassen et al., 1992; Drent et al., 1992). From these values, a Q of 0.81 was obtained by calibration in the present work and the metabolized energy by a Roseate Tern chick was estimated as

$$\text{ME} = \text{TotalFishEnergy} \times Q \quad (4)$$

with ME in kJ per chick d^{-1}.

2.5.2. Daily energy expenditure (EnExpend)

Not all metabolizable energy is accumulated as new body tissue or retained energy (RE). The rest of ME corresponds to metabolic heat production (H), which is the sum of energy required for basal metabolism (BM), biosynthesis of new tissue (E_{syn}), heat increment (HI), thermoregulation (TR) and activity (A) (Weathers, 1996).

Based on the allometric relation for hatchling basal metabolic rate (BMR_h) found by Klaassen and Drent (1991), the model assumes a basal metabolic rate (kJ h^{-1}) described by

$$\text{BMR} = 0.047 \times \text{Weight}^{0.85} \quad (5)$$

where Weight is the average weight of a Roseate Tern chick (g) and BMR is transformed to g wet weight d^{-1} for units consistency.

No real data were available to describe explicitly the amount of energy wasted by chicks with E_{syn}, HI, TR or A, but a value of $0.43 \times$ BMR was obtained by calibration. On the other hand, such as previously used in other works (e.g. Riddington et al., 1996; Stock and Hofeditz, 1997; Reuter and Breckling, 1999), in this work, the energetic costs of different behaviours is expressed as a multiple of basal metabolism. Thus, the daily energy expenditure by a chick (EnExpend, g ww d^{-1}), including energetic wastes with basal metabolism plus other unspecified losses (e.g. activity, thermoregulation, etc.), is calculated by

$$\text{EnExpend} = \text{BMR} + 0.43 \cdot \text{BMR} = 1.43 : \text{BMR} \quad (6)$$

2.5.3. Roseate Terns chick's weight

The average weight (g wet weight) of a Roseate Tern chick from hatching to fledging is calculated by

$$\frac{\partial \text{Weight}}{\partial t} = \text{EnIn} - \text{EnExpend} \quad (7)$$

Hatching weights, which are the initial values of the state variable, correspond to real values and were 15.4 and 14.5 g for 1995 and 1996, respectively.

3. Results

For 1996 predicted weight variation of Roseate Tern chicks is very close to the real variation (Fig. 5A). Both curves follow the same type of pattern, characterised by high initial growth rates, which slow down in the

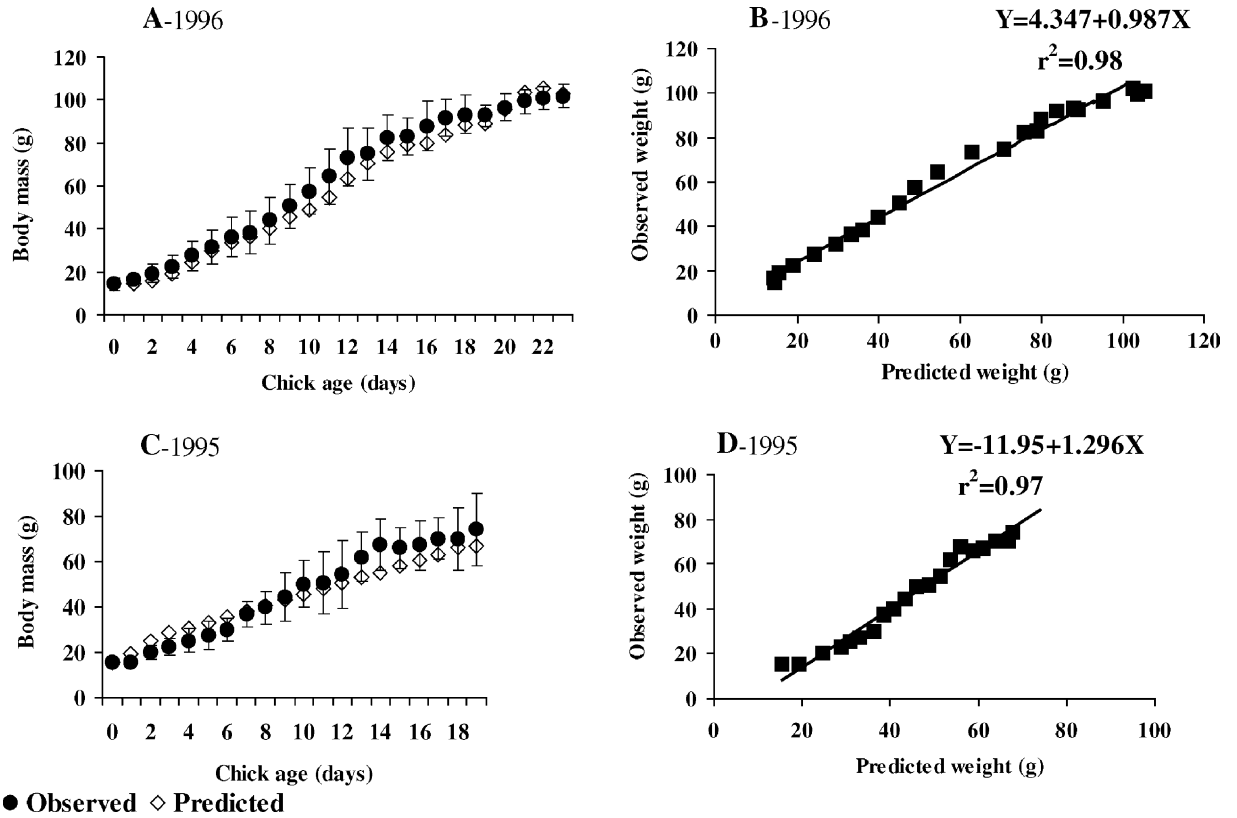

Fig. 5. Observed (±standard deviation) and predicted Roseate Tern chick's growth from hatching to fledging in 1996 (A) and in 1995 (C) and regression line between observed and predicted chick's weight in 1996 (B) and 1995 (D). Regression equations and r^2 are also shown. The regression equation for 1996 (B) has a slope which is not significantly different from 1 and an intercept which is not significantly different from 0 (DBK-regression test, $N = 24$, $F_{2,22} = 1.221$, $P < 0.001$).

last days. Most of the predicted values are within the standard deviation bars of the observed results. The regression line (Model II-regression) between observed and predicted results is highly significant (ANOVA, $F_{1,22} = 1418$, $P < 0.001$, $r^2 = 0.984$). Furthermore, the slope of the regression is not significantly different from 1 and the intercept is not significantly different from 0 (DBK-regression test, $F_{2,22} = 1.221$, $P < 0.001$) (Fig. 5B).

The regression between predicted and observed data in 1995 is also significant (ANOVA, $F_{1,19} = 559.1$, $P < 0.001$; $r^2 = 0.967$), although the slope of the regression is significantly different from 1 and the intercept is significantly different from 0 (DBK-regression test, $F_{2,19} = 31.483$), which reflects the discrepancies between observed and predicted Roseate Tern weight (Fig. 5C and D).

Sensitivity analysis of the extra energy expenditure parameter (Fig. 6A), of the assimilation coefficient (Fig. 6B) and of chicks initial weight (Fig. 6C) shows that the assimilation efficiency is the most sensitive parameter because a ±10% variation of its value causes a ±10 variation on chicks weight at 23 days. Only a variation of ±50% of extra energy expenditure causes a variation of approximately ±10% on chicks weight at 23 days. The sensitivity of both parameters increases with time, with increasing chick's weight, while the model sensibility to the tested range of initial weight variation is very low.

Assuming a constant ingestion rate of 4.5 fish per chick d^{-1} and a constant average length for each fish species obtained from real data, the model predicts that only the chicks feeding on *T. picturatus*

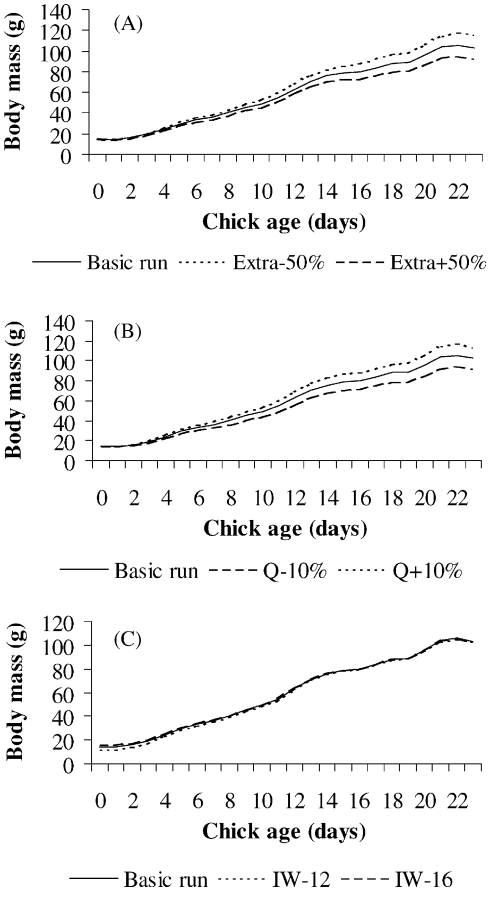

Fig. 6. Model sensibility to a variation of ±50% in the extra energy expenditure parameter (A), to a variation of ±10% in the assimilation efficiency (*Q*) (B) and to different initial (at hatching) weights (IW) of chicks (12 and 16 g) (C). The basic run corresponds to the model run using data from 1996.

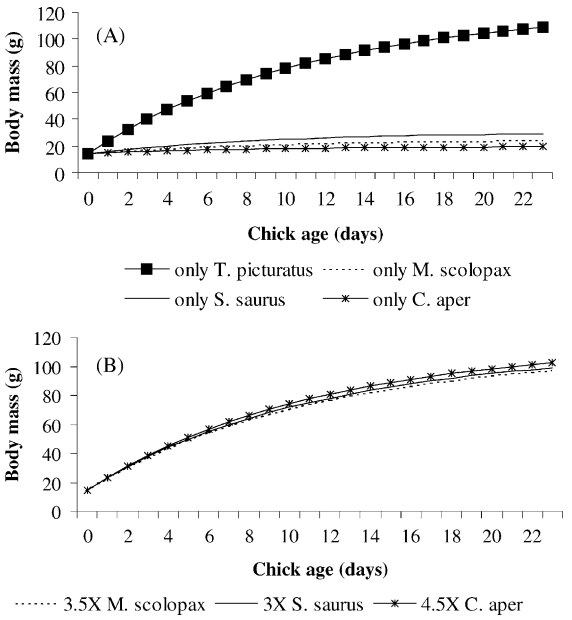

Fig. 7. Effects of the most abundant fish prey species on the growth of Roseate Tern chicks. (A) The model was run separately for each fish species. In every run, a constant ingestion rate of 4.5 fish per chick per day and a constant length, based on real data, for each fish species were used. Average length: *T. picturatus*: 8.85 cm, *M. scolopax*: 6.80 cm, *S. saurus*: 8.31 cm, *C. aper*: 4.30 cm. (B) Compared to the previous runs, chick's ingestion rate must increase by 3.5, 3 and 4.5 fold of *M. scolopax*, *S. saurus* and *C. aper*, respectively, to reach a weight of approximately 100 g at fledging.

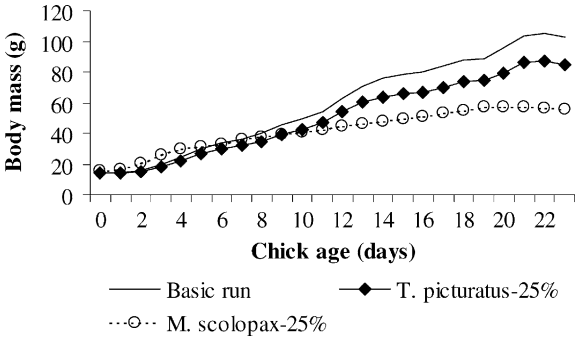

Fig. 8. Roseate Tern growth after a reduction of 25% on *T. picturatus* (energetically rich prey) abundance and after a reduction of 25% on *M. scolopax* (energetically poor prey) abundance. The simulation with *T. picturatus* runs with data from 1996, while the simulation with *M. scolopax* runs with data from 1995. The basic run corresponds to the model run using data from 1996.

with an average length of 8.71 cm, show a normal growth variation and reach a weight of approximately 100 g after 23 days, while chicks fed on the other three main fish species (*S. saurus*—average length = 8.31 cm, *M. scolopax*—average length = 6.80 cm, *C. aper*—av. length = 4.30 cm) are almost unable to grow (Fig. 7A). In such a situation, to exhibit a normal growth variation and reach a weight of approximately 100 g after 23 days, Roseate Tern chicks would need to increase their ingestion rates by 13.5, 15.75 and 20.25 fish per chick d^{-1} for *S. sauri*, *M. scolopax* and *C. aper*, respectively (Fig. 7B).

The model shows that chicks with 23 days of age will attain 85 and 56 g, according to a 25% reduction in prey within a year of energetically more (*T. picturatus*) and less (*M. scolopax*) favourable prey, respectively (Fig. 8).

4. Discussion

In the present work, the energy input calculations result from real data based on ingestion rates of fish species, per chick, per day, and on the measured lengths of ingested fishes, while the energy expenditure was defined as the basal metabolic rate plus an additional term accounting for other energetic wastes, described as a BMR multiple, and obtained by calibration. Although expressing the energetic costs of different behaviours as multiples of basal metabolism has previously been used in several other studies (e.g. Riddington et al., 1996; Stock and Hofeditz, 1997; Reuter and Breckling, 1999), as well as, using unmeasured estimates of BMR and of individual activities (in Ellis and Gabrielsen, 2002), these approaches must be seen cautiously since they can never replace actual measurements (Ellis and Gabrielsen, 2002). Furthermore, as expected for an energetic balance model, the sensitivity analysis showed that the assimilation efficiency (Q) and the energy expenditure (EnExpend) parameters are highly sensitive and, consequently, small variations of its values cause significant differences in Roseate Tern growth. On the other hand, intraspecific variations in chick growth and nestling success occur due to several factors, such as timing of egg laying, age and breeding experience of the parents, weather conditions or individual quality genetically determined (Visser, 2002). For these reasons, the application of the present model to other Roseate Tern populations must be done cautiously and taking into account its limitations, namely those related to parameters of energy expenditure. In fact, the present model may be further improved and its predictions more accurate, if the parameters related to chick energy waste are known accurately for the modelled population. As in the present work, in a model of behavioural energetics of American robins, Marcum et al. (1998) also described the daily energy expenditure as the basal metabolism plus other terms defined as multiples of BMR. However, instead of defining a general term to account for unspecific wastes as in the present work, Marcum et al. (1998) described the energetic wastes with perching, eating and flying based on data found in the literature. Although more discriminative, such approach may be more adequate to adult birds than to altricial birds before fledging, which show limited activity. On the other hand, while energy for maintenance (BMR and thermoregulation) is obligatory, the energy expended on activities such as flying or foraging are sensitive to behavioural shifts (Walsberg, 1983), suggesting that this value may vary significantly from one population to another or even within the same population from one season to another.

Nevertheless, when compared with real data, model results were very satisfactory, namely, the predictions for 1996. Although model predictions for 1995 followed the same general pattern as the observed data,

the regression between the two sets failed to show a slope of 1 and an intercept of 0. Among other causes, this may be related with the fact that, the caloric content of fishes was assumed to be equal to 1996. Additionally, the model was calibrated with data from 1996 and, in 1995 although the experimental procedure was similar to that of 1996, chicks were kept inside a smaller experimental area. This difference may have caused different energy expenditure values by the chicks in 1995 and 1996, which could not be accounted for by the model.

From the four main prey species available for Roseate Tern in the Azores in 1996, *T. picturatus* with an average length of 8.71 cm was the most energetically favourable item. This can be attributed both to both to the length–weight regression of *T. picturatus* and to the capacity of Roseate Tern chicks to swallow *T. picturatus* with an average length of 8.71 cm. Although *C. aper* shows an higher length–weight relationship than *T. picturatus*, Roseate Tern chicks only seem able to ingest *C. aper* items with less than 5 cm, because this species is wider than *T. picturatus*. In fact, until the age of 6 days, the ingestion rate of chicks depends on fish shape (young birds ingest only thinner prey, Ramos et al., 1998b). Thus, it is energetically more advantageous for a chick to be fed a *T. picturatus* with 8.71 cm than a *C. aper* with 4.30 or 4.37 cm (which were the average lengths of *C. aper* in 1996 and 1995, respectively). In the case of *S. saurus* and *M. scolopax*, a certain length of these two fish species is not as efficient as *T. picturatus*, because of their lower length–weight relationship. Our results suggest that this point should explain the predicted and observed data in 1995. The significantly higher ingestion rates of chicks in 1995 compared to 1996 may be related with an increase in the energetic value of prey items from 1995 to 1996, corresponding to a switch from *M. scolopax* to *T. picturatus*. The availability of mostly less energetic fish such as, *M. scolopax*, apparently leads to higher delivery rates by the parents and, consequently, to higher ingestion rates by the chicks. However, both observed data and model predictions suggest that, in spite of such increases, at least in certain years, the growth efficiency is lower than when the chicks were fed with *T. picturatus* with an average length of 8.71 cm. Therefore, the existence of low energetically prey fish may have important consequences for the growth and survival of Roseate Tern populations in the Azores, both due to the higher energetic demand on the parents and to the lower growth rates of the chicks. Dahdul and Horn (2003) raised chicks of Elegant terns (*Sterna elegans*) in the laboratory on three diets differing in energy content and showed that terns have evolved certain capacities in growth and digestion that may increase the probability of chick survival, such as faster gut-passage rates for chicks fed on low-energy fish. However, chicks raised on a lower quality diet were underweight at fledging, which is similar to the results provided by our model. When seabirds fledge underweight their post-fledging survival is likely to decrease (Perrins, 1966). Additionally, the significant increase in parental effort to increased begging for food by chicks fed on lower quality diet may be reflected on long-term reproductive success because parents with poor body condition are more likely to defer breeding in some years (Chastel et al., 1995; Catry et al., 1998). Furthermore, according to the model, only *T. picturatus* with a length $\geq$8.5 cm can sustain a weight at fledging of 100 g, assuming a constant ingestion rate of 4.5 fish per chick d^{-1}. Thus, depending on the most abundant prey and on its average length (which besides determining its energy, it will also determine if chicks are able to ingest it or not), in some years, Roseate Terns may be able to maximize their energy uptake by delivering energetically rich fish to the chicks and decreasing the capture rates. In years with a dominance of low energetic prey, both the high capture rate by parents and delivery rate to chicks will decrease the total energy available for the breeding population.

Apart from the impact caused by different quality prey items, there may be also an impact associated to fish stock reductions. The model shows that chicks with 23 days of age will attain 85 and 56 g, according to a 25% reduction in prey within a year of energetically more and less favourable prey, respectively. Because terns allocate energy preferentially towards wing development (Dahdul and Horn, 2003), chicks in the first situation are still likely to fledge. On the contrary, the models shows that a reduction of 25% in the supply of fish, in a year with energetically less favourable preys, will certainly compromise chick survival.

In summary, the growth of Roseate Tern chicks in the Azores will be significantly reduced in response to a decrease in energy intake resulting from provi-

sioning of low quality fish species and clutch survival is compromised whenever this factor is associated to significant (25%) fish stock reductions.

Moreover, the model developed in this work proved to be a highly dynamic tool in assessing variations in postnatal growth of Roseate Tern chicks in response to variations in food quality and quantity. Such approach can represent a valuable complementary approach to more rigid and difficult laboratory works. Thus, energetic models of seabird populations may be of high value to the conservation strategies of these species. Changes in the abundance and availability of fish resources due to anthropogenic influences throughout the world is likely to offset the optimal provisioning of marine terns, that must find food resources for breeding within a small range (Craik and Becker, 1992).

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